THE EFFECT OF TEMPERATURE ON THE WINGS OF DIMORPHOS/DIMORPHOS VESTIGIAL–PENNANT/VESTIGIAL IN DROSOPHILA MELANOGASTER

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Harnly (1930b) and Stanley (1931) showed a critical temperature for the increase in wing size of the homozygous vestigial flies. This response is direct but not proportional to the rise in temperature. It was found that the introduction of the sex-linked modifier dimorphos into this genotype lowered the critical temperature for wing enlargement 5° C. for the males and 2° C. for the females (Harnly and Harnly, 1935). Again the response was direct but not proportional throughout the viable temperature range. Vestigial-pennant is a reverse mutation from vestigial to a recessive wild type allele. The wings of these flies showed an inverse response to temperature, and a critical point appeared to occur between 28° and 30° (Harnly and Harnly, 1936). It was also found that the heterozygous vestigial-pennant/vestigial wings showed an inverse response to temperature from 16° to 22° and a direct response from 26° through 32°.

These shifts in critical temperatures, the direct or inverse response of wing size to temperature of the homozygotes, and the apparent reversal of dominance with temperature in the heterozygote led to this study of the dimorphos/dimorphos vestigial-pennant/vestigial genotype.

STOCKS AND METHODS

Through a knowledge of the phenotypes produced by dimorphos vestigial, homozygous vestigial-pennant and the heterozygous vestigial/vestigial-pennant at 22° and 25°, it was possible to develop a stock of dimorphos vestigial-pennant. Isogenic stocks of dimorphos vestigial and dimorphos vestigial-pennant were employed in these experiments. Due to the breeding technique (Harnly and Harnly, 1935, 1936) these stocks differ from each other in genotype only at the vestigial locus.

The culture methods, procedure for measurement of wings, etc. were the same as those described in earlier papers of this series (Harnly, 1932, 1936; Harnly and Harnly, 1935). Homozygous dimorphos vestigial-pennant females were mated to homozygous dimorphos vestigial males. Their offspring (dimorphos/dimorphos vestigial-pennant/vestigial) were allowed complete development at 16°, 18°, 20°, 22°, 24°, 26°, 28°, and 30° C. Those F_1 individuals placed at 32° for development were returned to a 26° incubator after the completion of five days (120 hours) of development and there completed their growth and their emergence.

RESULTS

Wing length

The genes used and their symbols are: vestigial (vg), vestigial-pennant (vg^p) and dimorphos (di). The curves for the mean wing length for the di/di vg^p/vg

males and females show an inverse response to temperature increases from 16° to 28°, and are similar in slopes and values to those previously recorded for the wild type (Stanley, 1935) and homozygous vg^p (Harnly and Harnly, 1936). The mean wing lengths in mm. of di/di vg^p/vg males and females are shown in Table I.

TABLE I

Mean wing length in mm., di/di vg/vg^p., 5 trials

° C.	Males				Females			
	Length	±	P.E.	σ	Length	±	P.E.	σ
16°	2.53	±	0.0097	0.1241	2.60	±	0.0089	0.1135
18°	2.49	±	0.0056	0.0724	2.59	±	0.0103	0.1306
20°	2.42	±	0.0055	0.0707	2.53	±	0.0086	0.1101
22°	2.32	±	0.0082	0.1030	2.43	±	0.0119	0.1524
24°	2.25	±	0.0069	0.0897	2.33	±	0.0121	0.1550
26°	2.25	±	0.0066	0.0755	2.35	±	0.0109	0.1257
28°	2.11	±	0.0073	0.0939	2.27	±	0.0094	0.1205
30°	2.15	±	0.0067	0.0859	2.28	±	0.0067	0.0864
32°	2.24	±	0.0081	0.0969	2.32	±	0.0069	0.0886

The di/di vg^p/vg males and females show a gradual decrease in wing length from 16° to 28° beyond which there is a gradual increase in wing length to 32°. Apparently 28° is a critical point since the slope is negative below this temperature and is positive above it. The female wings are consistently longer than those of the males throughout the temperature range. The similarity in slopes and values of the di/di vg^p/vg male and female curves indicates there was no difference in the response of the two sexes in wing length over the range employed.

Wing area

The mean wing areas for di/di vg^p/vg will be found in Table II and are shown

TABLE II

Mean wing area in sq. mm., di/di vg/vg^p., 5 trials

° C.	Males				Females			
	Area	±	P.E.	σ	Area	±	P.E.	σ
16°	1.591	±	0.0090	0.1451	1.327	±	0.0171	0.2161
18°	1.555	±	0.0071	0.0914	1.171	±	0.0171	0.2168
20°	1.482	±	0.0086	0.1106	1.065	±	0.0151	0.1934
22°	1.338	±	0.0086	0.1080	0.964	±	0.0156	0.2006
24°	1.278	±	0.0219	0.2313	1.063	±	0.0200	0.2568
26°	1.267	±	0.0064	0.0730	1.111	±	0.0163	0.1867
28°	1.138	±	0.0080	0.1026	1.219	±	0.0116	0.1492
30°	1.214	±	0.0062	0.0796	1.294	±	0.0065	0.0840
32°	1.291	±	0.0080	0.0957	1.342	±	0.0093	0.1192

in Figures 1 and 2 together with those of Harnly (1930b) and Harnly and Harnly (1935, 1936) for the genotypes indicated.

The male curves for vg^{p} and di/di vg^{p}/vg coincide and have a negative slope between 16° and 28°. Between 28° and 32° they diverge sharply, the homozygote having a higher negative value while the heterozygote has a definitely positive slope. Apparently 28° is the critical point for length and area in the males of both genotypes.

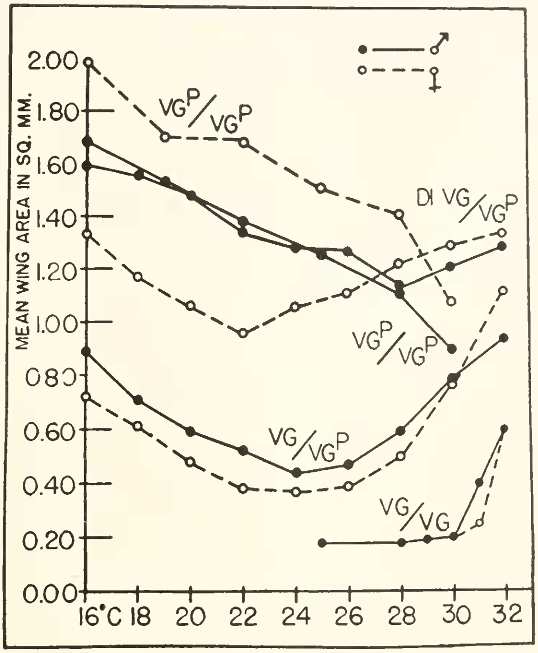

FIGURE 1.

The curve for the di/di vg^{p}/vg female wing area is U-shaped as is that of vg^{p}/vg females between 16° and 32°, but their wings are approximately double the area of the vg^{p}/vg wings. From 16° to 22° there is a gradual decrease and from 22° to 32° there is a steady increase in the area of the di/di vg^{p}/vg female wings. The reversal in the sign of the slope of the curve at 22° demonstrates that this is the critical temperature for the di/di vg^{p}/vg females. Between 26° and 28° the female curve crosses the male curve indicating a larger wing area for the females beyond that point up to 32°.

SHIFT IN WING FORM THRESHOLD

The male wing phenotype did not vary significantly from 16° to 32° in the di/di vg^{p}/vg flies. However, this genotype appears to be responsive to temperature, in that the percentage of perfect wings varied with the temperature. Wings with minor nicks were produced at all temperatures, but perfect wings were only produced at 16° (19%), 18° (11%), 26° (10%), 28° (7%), 30° (7%), and 32° (28%).

The original homozygous vg^p stock showed only occasional nicks in the distal margins of the wings (Harnly and Harnly, 1936). Repeated back crossing of the vg^p to the inbred vg stock has introduced one or more wing margin genes intensifying this tendency. This resulted in a vg^p stock that regularly showed minor nicks at all temperatures, but produced perfect wings at 16° (Harnly and Harnly, 1936). Due to their origin the homozygous di vg^p and the homozygous di vg stocks presumably carried the same wing margin gene or genes for the production of these minor nicks or notches.

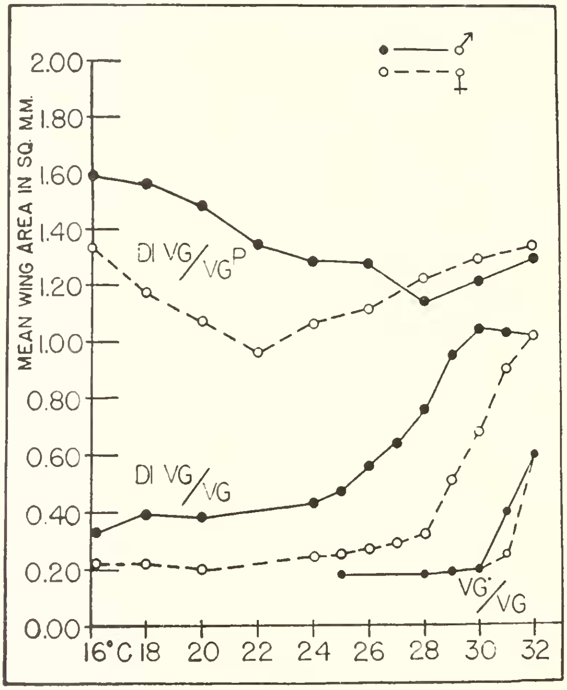

FIGURE 2.

The variation in frequency of nicks through the visible temperature range indicates that the wing-margin gene or genes are thermolabile at some period during the development of the individual. The largest number of perfectly normal wings appear at the temperature extremes, namely 16° and 32°. The smaller percentages of normal wings are found at temperatures close to the upper extreme. This indicates that some genes affecting wing margins are expressed at low temperatures while others find expression at high temperatures. Harnly (1942) obtained parallel results from reciprocal crosses between the two vg^p stocks and between these and a new vg^p stock. The di/di vg^p/vg genotype evidently produces full wings in the males with the possibility of minor variations at the distal end through the action of these wing-margin genes.

The di/di vg^p/vg female wings offer an entirely different picture. From 16° through 26° the phenotype varied around over-sized "antlered" with the occasional appearance of a "strap" wing. At 24° and at 26° phenotypes resembling the vestigial alleles antlered, snipped, carved and notched also appeared; from 28° to 32° the wings were predominantly "notched" to "nicked." Perfect normal wings appear only at 32° and 24 per cent of these wings were normal.

The di/di vg^p/vg female wings at 16° were similar to the male wings of the vg^p/vg described by Harnly and Harnly (1936) at 16°. The introduction of di into the vg^p/vg genotype has lowered the threshold for the wing pattern sequence previously described (Harnly and Harnly, 1935). This results in a pattern grade (antlered) for the female at 16° the equivalent of that first observed between 28° and 30° in the genotype (female vg^p/vg) carrying the normal allele of this sex-linked modifier (Harnly and Harnly, 1936). At these higher temperatures the di/di vg^p/vg females graded phenotypically "notched" to "nicked." The di gene had lowered the pattern threshold some 12° in the females and had lowered it so far in the males that only the full-wing pattern grade was produced throughout the viable temperature range.

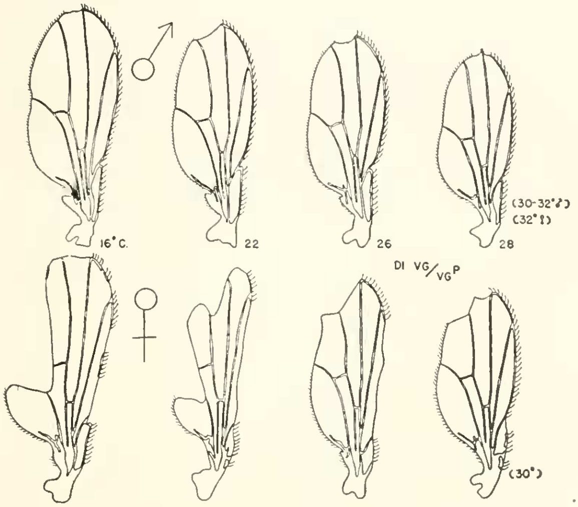

FIGURE 3.

SHIFTS IN THE CRITICAL TEMPERATURE

The di mutation arose in an inbred homozygous vg stock and consequently the di vg genotype differed from this inbred vg strain only in the allele present at the di locus. The original vg^p mutant arose in a culture of black vestigial flies. This mutant had been backcrossed for many generations to the inbred vg stock. This produced a vg^p line differing from the inbred vg strain by only the allele at the vg locus. Therefore, these three genotypes differed only by known alleles at the vg and di loci. Consequently the introduction of di into this backcrossed vg^p stock produced a change in only one locus. The experiments on vg, di vg, vg^p/vg and vg^p (unpublished) have been reported previously (Harnly, 1930, 1936; Harnly and Harnly, 1935, 1936). Including our own experiments on di/di vg^p/vg truly comparable data is now available on five isogenic genotypes.

The di/di vg^p/vg male wings are phenotypically wild type throughout the temperature range employed. However, as mentioned above, "nicks" occasionally appear at the distal margins of the wings. These "nicks" are due to wing-margin genes (Harnly, 1942). The curves for male wing length and wing area coincide with the wild and vg^p curves and demonstrate a similar response to temperature between 16° and 28°. The reversal in the sign of the slope of the di/di vg^p/vg curves between 28° and 32° is markedly contrasted with the further fall of the wild and vg^p curves. This response is due to the combined action of the di and vg genes as will be shown later. The female length curve of di/di vg^p/vg parallels that of the males throughout the temperature range. Evidently under the conditions in these experiments, the threshold for the wild phenotype and temperature reactions of the male and the length response for the female has been reached in this genotype.

The critical temperature is a function of the genotype. The response of vg is direct with temperature and the value of the slope of the curve increases sharply above 30°. The di gene lowers this critical temperature 2° in the homozygous vg female. The slope of the wing area curve of homozygous vg^p females is negative in sign. The wing area curve of the heterozygote vg^p/vg has a negative slope from 16° to 24° and a positive slope from that point to 32°. The area curve of the di/di vg^p/vg females has a negative slope from 16° to 22°, and a positive slope from there to 32°. Again, the introduction of the dimorphos gene has lowered the critical temperature 2°, in the females.

These shifts in the critical temperature from genotype to genotype may be explained as the result of changes in dominance. On that basis the critical temperature (e.g. 24° for vg^p/vg) is the point at which a reversal in dominance occurs between the alleles vg^p and vg in the heterozygote as was suggested earlier by Harnly and Harnly (1936). The data from these experiments with di/di vg^p/vg indicate that there may be two critical temperatures: (1) the reversal of dominance as indicated in the wing area curves; and (2) the phenotype threshold (discussed above), a problem of differentiation as opposed to that of growth in development. It may be that further work will show that both of these are different manifestations of the same phenomenon.

SUMMARY

1. The genotype di/di vg^p/vg was examined at 2° intervals from 16° to 32°.

2. The length of the wings on the males and the females decreased from 16° to 28° and increased from 28° to 32°. The wings of the females were longer than those of the males at all temperatures.

3. The area of the wings of the males decreased from 16° to 28° and then increased to 32°.

4. The critical temperature for both the length and area of the male wings is apparently 28°.

5. The area of the wings of the females decreased from 16° to 22° and increased from 22° to 32°. The resulting U-shaped curve is very similar to that reported

previously for vg^p/vg but the values are approximately double for the di/di vg^p/vg genotype.

6. The critical temperature for the female wing area appears to be at 22° and for wing length at 28°.

7. The di gene lowers the critical temperature for wing area 2° in the vg/vg female and the vg^p/vg female.

8. The critical temperature is a function of the genotype.

9. The males have wild type wings with minor marginal nicks at all temperatures. Wings with perfect margins were produced at 16° (19%), 18° (11%), 26° (10%), 28° (7%), 30° (7%), and 32° (28%). The marginal defects are obviously thermolabile.

10. The wings of the females varied around over-sized "antlered" with the occasional appearance of a "strap" wing from 16° to 26°. Phenotypes resembling the mutant alleles antlered, snipped, carved, and notched appeared at 24° and 26°. The wings were predominantly "notched" to "nicked" from 28° to 32°. Perfect margins were observed on twenty-four per cent of the wings developed at 32°.

11. The di gene lowered the wing pattern threshold some 12° in the females. In the males, this threshold was lowered below the viable range and only normal wings were produced.

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